but ruled that out. He then began to look in a wide range of other species and continued to find the same four-banded absorption spectrum. While examining a yeast preparation, he observed that immediately after shaking it, he failed to find the absorption pattern. Yet, "before I had time to remove the suspension from the field of vision of the microspectroscope, the four absorption bands suddenly reappeared" (Keilin, 1966, p. 145). Searching the published literature, Keilin discovered that Charles MacMunn had made the same finding in the 1880s (MacMunn, 1884; MacMunn, 1886). Keilin (1925) went beyond MacMunn's observation in determining that these bands came from three different hemochromogens which he labeled *cytochrome a*, *b*, and *c*. Each cytochrome itself was composed of at least one protein with an iron-porphyrin prosthetic group, with the iron atoms accounting for the reversible reactions. By 1939 Keilin, collaborating with Edward Hartree, had distinguished cytochrome a_3 from *a* and characterized the four cytochromes as forming a catalytic chain "which, by utilizing molecular oxygen, can easily oxidize to water certain hydrogen atoms in the substrate molecules activated by specific dehydrogenase systems" (Keilin and Hartree, 1939, p. 190). They named the enzyme catalyzing this oxidation *cytochrome oxidase*. Based in part on their identical absorption spectra, Keilin and Hartree identified cytochrome oxidase with Warburg's *Atmungsferment*. They also tentatively identified it with cytochrome a_3 in particular, but commented that the b-c-a-a_3 system could be regarded as either three hydrogen carriers plus an enzyme or as a four-component chain of enzymes (Keilin & Hartree, 1939). In the 1940s, this reaction sequence was referred to as the *respiratory chain*. Later, the term *electron transport chain* became favored as biochemists discovered additional components and also wished to emphasize that it was pairs of electrons – dissociated from the protons of the hydrogen atom – that were transported down an energy gradient to molecular oxygen.

In his 1932 Nobel lecture Warburg (1932) insisted that *Atmungsferment* was *the* active agent and resisted the claim that it was the cytochromes that were oxidized by activated oxygen. Nonetheless, during this period Warburg made two critical discoveries that filled in the steps between oxidation (dehydrogenation) of substrates and the oxidation-reduction reactions of cytochromes in the electron transport chain. I noted previously that in the mid-1930s Warburg and Christian discovered two coenzymes, which are now called NAD and NADP. In addition, they established that both NAD and NADP figure in connecting the oxidative reactions in the citric acid cycle to the electron transport chain. It took a number of years, though, for investigators to work out which of these two coenzymes participated in which reactions.